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Modeling the impact of climate change on a rare color morph in fish

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ABSTRACT

Species are typically comprised of a large number of genotypes, some of which are rare. Rare genotypes that are temperature-sensitive will predictably be impacted by climate change more profoundly than common genotypes for which gene expression does not depend on temperature. Computer simulations were used in this study to analyze the impact of changing temperatures on a very rare melanic morph that expresses a temperature-sensitive phenotype and is found in an abundant fish species *(Gambusia holbrooki)*. This numerical model assesses the frequency of the two natural color morphs, silver and black-spotted, over time and iterates in each generation, incorporating survival estimates for different life stages based upon data collected during empirical experiments. Using the current projections for mean surface temperature increase, which are 2.5° F to 10.4° F by the year 2100, the impact of warming environment on the mosquitofish population was analyzed. Three different climate warming scenarios were used to address annual temperature fluctuations and incorporate predicted temperature rise at correspondingly minimal, mid, and maximum levels. Our results indicate that increasing temperatures will seriously affect the rare color morph and in some cases will result in extinction. The minimal climate-warming scenario produced lower extinction risks for the rare morph; however, it still decreased the frequency of the rare genotype to minimal values. The mid-range warming scenario produced a higher risk of extinction, while the maximum warming scenario resulted in the extinction of the rare color morph. The results of this study shed light on the possibility that the effects of climate change may have important ramifications for rare genotypes in nature and will likely drive some rare species genotypes to extinction.

1. Introduction

The Earth's climate has changed since the preindustrial era and is projected to continue to change throughout the 21 st century. Global mean surface temperature is projected to increase over the next 100 years by up to 10.4 °F, and it has already warmed by 1.3° F over the 20th century (IPCC, 2007). Correlations between observed changes in climate and many factors such as survival, population size and distribution, reproduction time, and migration have been documented (Thomas et al., 2004). Studies using mid-range climate-warming scenarios and sample regions covering about 20% of Earth's terrestrial surface indicate that an estimated 15–37% of species and taxa in the studied regions may go extinct by 2050. This impact is anticipated to be greater if changes in climate are more extreme (Thomas et al., 2004). Recently, the thermal sensitivity of 2960 ray-finned fishes to future climatic exposure was investigated to find that fish will either migrate, adapt, or die off as temperatures continue to warm; this demonstrates that global patterns of vulnerability differ substantially between freshwater and marine realms (Comte and Olden, 2017).

Despite a voluminous literature on the impact of climate change, freshwater ecosystems have been relatively poorly studied. Heino et al. (2009) have shown that freshwater biodiversity is highly vulnerable to climate change, with extinction rates and extirpations of freshwater species matching or exceeding those suggested for better-known terrestrial taxa. Some evidence shows that freshwater species have exhibited range shifts in response to climate change in the last millennia, centuries, and decades. The proportion of potential losers (taxa becoming extinct) ranged from zero species for snails to 33% of the regional species pool for dragonflies. The set of potential winners (taxa becoming colonizers) was much larger, ranging from 53% for amphibians to 61% for dragonflies (Rosset and Oertly, 2011). However, these effects are typically species-specific, with cold-water organisms being generally negatively affected and warm-water organisms positively affected (Heino et al., 2009). Recent studies of freshwater invertebrates experimentally assessed the impact of altered temperature regimes on the emerging adults in aquatic insect communities. Experiments showed that mean body size decreased under warming conditions; however, the degree to which an organism's size was affected by

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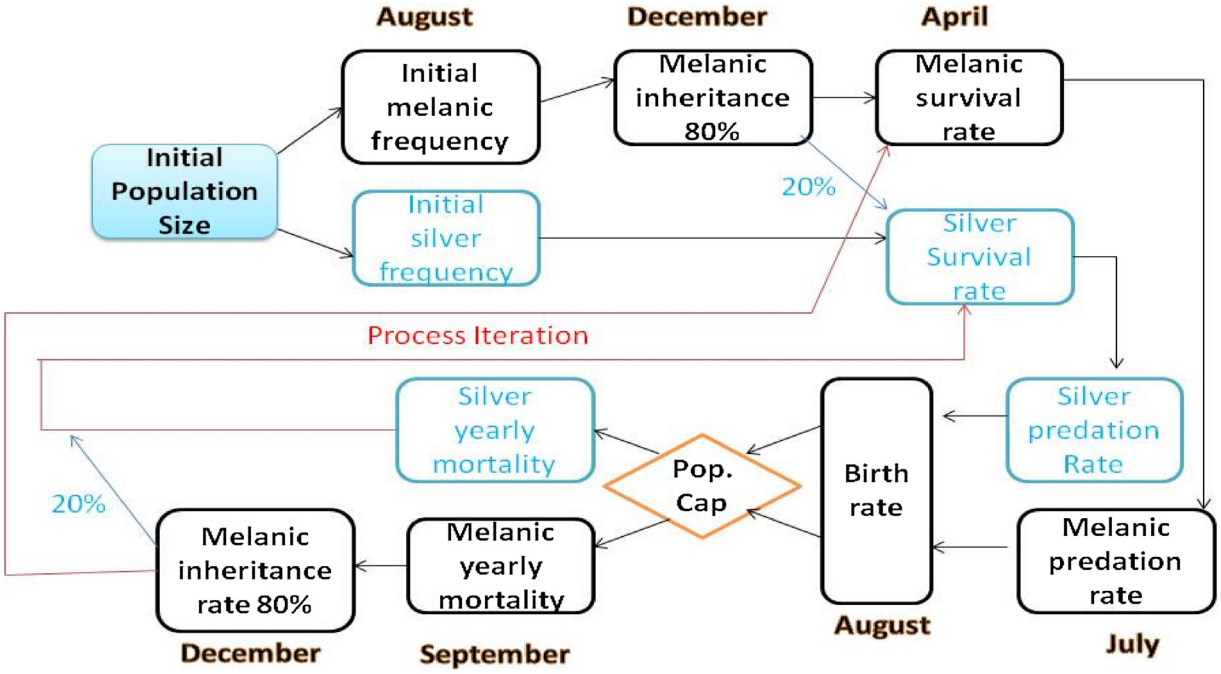

Fig. 1. The algorithm for the numerical model. The simulation begins with 'Initial Population Size' icon and the arrows point to the sequential changes affected in designated times (specific months) as the population ages and fitness changes occur for the color morphs.

temperature varied within and between taxa (Sardiña et al., 2017). These changes show the potential for changed temperature regimes to impact ecological systems at individual, population, and community levels, which in turn will affect the global biodiversity.

Long term preservation of biodiversity requires an understanding of the resistance of different species to environmental stress and particularly the impact of changing temperatures on ecological systems. The long time periods required to study the maintenance of rare genotypes in natural populations make numerical simulations an alluring option to field study when assessing long term changes in biological systems. Here we use numerical simulations to assess the impact of climate change on persistently rare genotypes in nature, as well as the populations that harbor them. We focus this study on Eastern Mosquitofish *(Gambusia holbrooki)*, which have a natural body color polymorphism wherein the rare morph is black-spotted and the common one is silver. Mosquitofish are small, live-bearing, freshwater fish that were commonly and widely introduced in US in early 1900s by the former U.S. Public Health Service, in large part because they were thought of as an effective and inexpensive way to control mosquitoes (Krumholz, 1948). More recent studies on mosquito control have not supported the view that *Gambusia* are particularly effective in reducing mosquito populations or in reducing the incidence of mosquito-borne diseases (Courtenay and Meffe, 1989; Arthington and Lloyd, 1989). Nevertheless, mosquitofish are widely spread in Atlantic and Gulf Slope drainages as far west as southern Alabama and as far north as Pennsylvania and New Jersey. Eastern Mosquitofish (*Gambusia holbrooki*) is native to the southeastern United States and shares a hybrid zone with *Gambusia affinis* (Western mosquitofish) around Mobile Bay, AL. The wild-type coloration of both species is silver, but small percentage of Eastern Mosquitofish express a rare but heritable melanic, black-spotted pattern that is not found in Western Mosquitofish.

The melanistic phenotype is almost entirely restricted to males and is inherited as a Y-chromosome-linked single-gene trait. Angus (1989) has shown that the Y-linked melanism allele (*M*) is temperature sensitive. It is dominant with high penetrance when fish are raised at 22 °C. Penetrance is much reduced, to about 42%, when fish are raised under warmer conditions (26 °C–29 °C) (Angus, 1989). Later Horth (2006) has shown that in some populations, 80% of males born to melanic sires turn melanic after at least 12 weeks of cold exposure. This expression pattern may result from the activation of a temperature-sensitive enzyme (e.g. tyrosine hydroxylase) (King et al., 1991). However, as Horth stated, "melanic inheritance is more complex than can be entirely resolved from the experimental design of this work…some populations have inducible melanism, others constitutive, therefore, more than one genotype produces the melanic phenotype" (Horth, 2006). In the short-term, genetic variability is often less critical than other determinants of population persistence (Lande, 1988). But over time, it can play the decisive role in allowing a population to persist and adapt in a changing environment (Lande and Shannon, 1996). As phenotypic expression of melanism in majority populations is directly affected by temperature and the consequence of loss of expression of melanism is the loss of fitness for the black male phenotype/genotype, the increasing temperatures as a result of climate change will directly affect melanic population.

Horth and Panayotova (2012) have shown that the persistence of the rare melanic morph is maintained through negative frequency dependent selection. Negative frequency dependent selection occurs when there is an advantage to being rare in a population, but this advantage decreases when the rare genotype increases in frequency (Cain and Sheppard, 1954; Ford, 1975; Sinervo and Lively, 1996). Although negative frequency dependence contributes to the persistence of melanic mosquitofish, as well as rare color morphs in other live-bearing fish, a rise in temperature will probably change the dynamics of this stable polymorphism (Rodd et al., 2002). The goal of this work is to use numerical simulations to study the long term effects of temperature changes predicted for the southeastern U.S. on the rare melanic morph and the mosquitofish population. Three different climate change scenarios were modeled: minimal (+4° F), mid-range (+8° F), and maximum climate-warming scenarios (+10° F). All relative fitness parameters for the two color morphs used in the simulations were obtained from empirical studies addressing natural selection (Horth and Travis, 2002; Horth et al., 2010).

2. Methods and materials

2.1. Algorithm

The algorithm used in the simulations, schematically illustrated in Fig. 1, models the life cycle of mosquitofish and was originally introduced in Horth and Panayotova (2012). Simulations are initiated in August of Year 1, when the largest pulse of young are born. All fish are born silver but eighty percent of F1 males born to melanic sires turn melanic after at least 12 weeks of cold exposure (Horth, 2006). This is incorporated in the model in December since that is about the time when fish born during the warmer months would express cold-induced melanism. Differential survival of the two morphs, which is contingent upon the frequency of melanic individuals in the population, is invoked in April (Horth and Travis, 2002). Differential survival related to predation is incorporated into the model in July, when the abundance of predators is high in nature. A differential birth rate is incorporated in the model in August, when the largest pulse of young is born in nature. The simulated population is then culled if it exceeded a carrying capacity and color morphs are culled proportionately. In September, the end of life mortality is invoked as adults die off after reproduction. This completes the life cycle of the fish and thus one generation of selection. All remaining individuals (juveniles maturing into adults) would then undergo differential selection regimes, contingent upon their color, as the next iteration of the model ensues.

To investigate the impact of climate change on the rare melanic morph and the mosquitofish population, the original model was modified as follows. Simulations were initiated in August with 10,000 individuals. An initial frequency of 0.06 was used for the population frequency of the melanic morph, since this was the equilibrium value at which the melanic morph stabilized in previous simulations (Horth and Panayotova, 2012). Next, the melanic inheritance rate applied in December was considered as a parameter, meaning that it was varied in different simulation runs to simulate different case scenarios that may result from the exposure of the rare morph to different environmental temperatures. Relative winter mortality was applied in April and relative effects of predation was applied in July. In August, the relative birth rates were applied for new, F1 juveniles. The carrying capacity of 100,000 individuals was checked and proportionate culling of the color morphs was applied if necessary. In September, annual mortality for adults (alive for one year) was applied, approximating a natural age structure. By the subsequent April, F1 juvenile fish matured and expressed their final body-color. In July, these F1 fish experienced differential predation. The model iterated for 10,000 total generations.

The initial population size of 10,000 individuals was selected because this allowed for population growth and seasonal fluctuation in population size, reflective of real world dynamics. The maximum population size (100,000 individuals) was based upon field observations and population size estimates for some lakes studied (Horth and Travis, 2002; Stewart and Miura, 1985). To incorporate novel autosomal mutation, one in 10^6 fish born to silver parents mutates to melanic and one in 10^7 fish born to a melanic mutates to silver; however, this may be conservative as most novel mutations are recessive (Schlager and Dickie, 1967).

One iteration of the model was equivalent to one calendar year, which reflects one generation for these fish. Simulations were run for 10,000 generations. The model was written in MATLAB (MathWorks Ver 7.10.0.499, R2010a) and all figures were created in MATLAB.

2.2. Parameters, equations and their derivations from empirical studies

As the equilibrium frequency for the melanic morph population was found to be 0.06, the parameter for the initial frequency of population-level melanism was set to 0.06 (Horth and Panayotova, 2012). The birth-rate was set to 2.3 percent, which was acquired from empirical work (Horth, 2006). Survivorship for melanic males was 0.81 when the population-level frequency of melanism was 0.033, and survivorship was 0.47 when population-level melanism was 0.083 (Horth and Travis, 2002). Based upon these data and additional lab studies, we assumed linear functional dependence between the two color morphs' survival rates (Horth et al., 2010). Therefore, to represent survival mathematically in our model, we assumed the two linear equations that best fit our data:

silver survival rate

$$\begin{cases} = \dfrac{0.05 * (\text{frequency of melanic males}) + 0.01452}{0.033}, & \text{freq. mel. males} \in (0,\ 0.033] \\ = \dfrac{-0.04 * (\text{frequency of melanic males}) + 0.02582}{0.05}, & \text{freq. mel. males} \in (0.033,\ 0.083] \end{cases}$$

melanic survival rate

$$\begin{cases} = 0.81, & \text{freq. mel. males} \in (0,\ 0.033) \\ = \dfrac{0.05172 - 0.34 * (\text{frequency of melanic males})}{0.05}, & \text{freq. mel. males} \in [0.033,\ 0.083] \end{cases}$$

Mathematically, the effect of predation on the above equations would be to alter the frequency of surviving silver and melanic fish. Relative differences in survival during predation for the two color morphs were taken from empirical trials with three different predators (Horth, 2004). For this work, we used the empirical data and determined a relative predation ratio of 17 melanic: 83 silver males.

All fish are born silver but about 80% of F1 males born to melanic sires would express melanic color after about 12 weeks of cold exposure. As this fish lives generally in tropical climate areas, increasing mean surface temperatures as a result of climate change will shorten the length of cold-water exposure and cause melanic response to vary. To explore the sensitivity of the melanic morph population to the increasing temperatures, melanic inheritance was considered as a parameter (called latter inheritance parameter) and assumed to vary inversely with respect to temperature, meaning that as mean temperature increases the percentage of fish turning melanic decreases. This assumption is based on the study by Angus (1989), who observed that the percentage of melanic expression in the black-patterned rate morph decreased when the fish were raised in warmer environmental temperatures. Based on the 2007 IPCC Fourth Assessment Report, three different climate change scenarios were explored: minimal, mid-range, and maximum climate-warming scenario (IPCC, 2007). For the minimal climate-warming scenario, it was assumed that the mean temperature will rise by 4° F over the next 100 year; for the mid-range, an 8° F increase was assumed; and for the maximum-range scenario, a 10 °F average increase was assumed. In addition, for each climate-warming scenario, four different relationships between inheritance parameter and increasing temperatures were considered, particularly 1%, 2.5%, and 5% change in melanic inheritance parameter per each degree Fahrenheit change in temperature.

Year one of the model was initiated with the average low winter temperature of 42° F derived as the mean low winter temperature for Northern Florida for the last 10 years (National Oceanic and Athmospheric Administration (NOAA, 2015). To model natural fluctuations in temperature from year to year, MATLAB's random number function was utilized and the standard deviation for the temperature in Florida, ± 0.9Fo (Maul and Sims, 2007) was used. This stochastic process created annual temperatures that increase or decrease from year-to-year while simultaneously a gradual steady increase in average temperature occurs over a 100 year period according to the minimal-, mid-, or maximum-warming scenarios. After that, a stabilized mean temperature was assumed and total of 10,000 years were simulated.

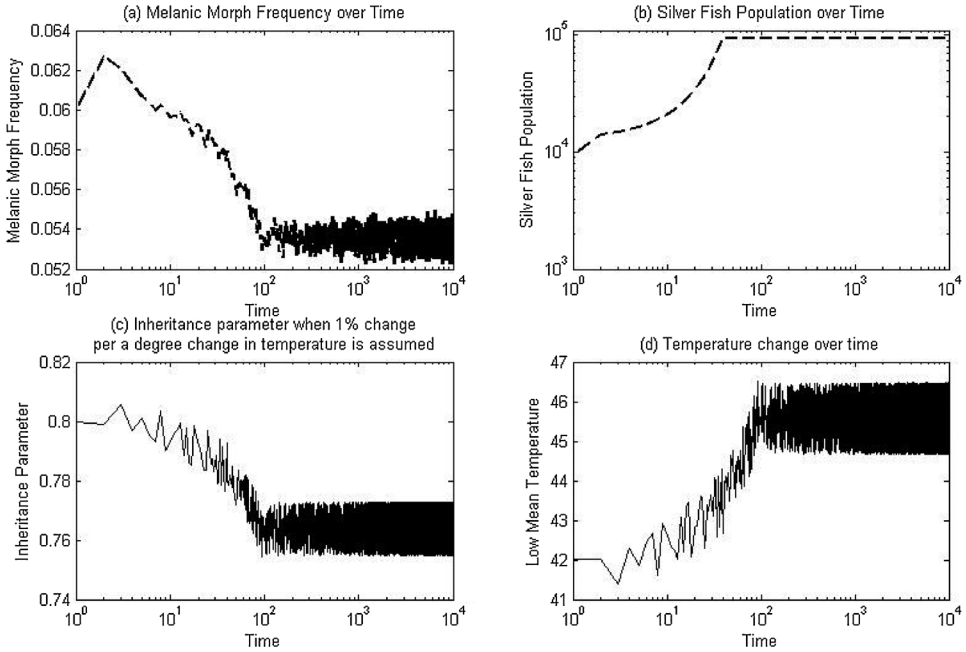

Fig. 2. (a) melanic morph frequency over time; (b) silver population over time; (c) the inheritance parameter change over time when 1% decrease in inheritance parameter per every 1° F increase is assumed; (d) temperature change over time starting from 42° F and gradually increasing to 46° F over the first 100 years.

3. Results

3.1. Minimal climate-warming scenario

Three different relationship scenarios for the dependence of the inheritance parameter on cold-temperature exposure were assessed, particularly 1%, 2.5%, and 5% decrease in the melanic inheritance per 1° F increase in mean surface temperature was assumed. Fig. 2 illustrates the result when 1% decrease in inheritance parameter of the melanic morphs per 1° F temperature change was assumed. The change in the inheritance parameter for the melanic morph varied according to Fig. 2(c) correlated to the mean temperature variation given in Fig. 2(d). All simulations were initiated with the 0.06 melanic morph frequency, which was the equilibrium value for this color morph. As it can be seen in Fig. 2(a), melanic frequency decreased significantly to a level slightly higher than 0.05 over the first 100 years when the mean temperature increased to about 46° F. Silver fish populations were not affected by the increasing temperatures. As it was mentioned by Heino et al. (2009), the effects of climate warming are species-specified, with cold-water organisms being generally negatively affected and warm-water organisms positively affected; our simulations support that statement. Even though the mosquitofish is a warm-water organism, melanic morph needs certain cold exposure for the expression of the melanism and hence it is negatively affected by the general temperature increase.

As Fig. 3 shows, when 2.5% decrease in the inheritance parameter was assumed per each degree change in temperature, the melanic frequency stabilized at an even lower level of about 0.04 (see Fig. 3(b)) while with a 5% decrease, melanic morph became extinct for about 100 years (see Fig. 3(c)). Any further decrease in the inheritance parameter resulted in extinction of the melanic morph for a shorter period of time.

3.2. Mid-range climate-warming scenario

To simulate a mid-range climate warming scenario, it was assumed that temperature will increase on average with 8 degrees Fahrenheit over the next 100 years, raising the low average temperature from 42° F to 50° F. As depicted in Fig. 4(a), if there is 1% decrease in melanic inheritance per every degree of temperature increase, melanic morph stabilized at a significantly lower frequency of about 0.043. Any further decrease in the inheritance parameter resulted in extinction of the rare color morph (see Fig. 4(b) and (c)).

3.3. Maximum climate-warming scenario

To simulate a maximum climate warming scenario, it was assumed that temperature will increase on average with 10 degrees Fahrenheit over the next 100 years, raising the low average temperature from 42° F to 52° F. In this case scenario, simulations show that even a slight decrease in the melanic inheritance will have a significant impact on the rare melanic morph. As we can see in Fig. 5(a), melanic morph frequency stabilized at 0.033, the lowest frequency that this morph occurs at in nature, when an 1% decrease in the inheritance parameter was assumed. Any further decrease in the inheritance parameter resulted in the extinction of the melanic fish population (Fig. 5(b) and (c)).

4. Conclusions and discussions

Heat resistance, which is important for adapting to temperature change, is known to be especially high in *Gambusia* (Al-Habbib and Yacoob, 1993). However, numerical simulations performed in this study show that silver and melanic morphs will be affected very differently by the increasing temperatures as a result of climate change. Even the most conservative estimates for climate-warming scenarios will have a significant impact on the melanic population, who may even go extinct. Despite this, our simulations also suggest that if temperature stabilizes before melanic mosquitofish go extinct, their population may recover to some degree. In contrast, the model shows that the silver mosquitofish population steadily increases and reaches the carrying capacity.

Natural selection acts differentially on silver and melanic eastern male mosquitofish; melanic mosquitofish are subjected to a lower predation rate (and higher recapture rate in nature) than silver males (Horth, 2004) and negative frequency-dependent survival is also associated with melanism in this species (Horth and Travis, 2002). However, when concerning heat resistance, melanism appears to be disadvantageous. In addition, melanic males have reduced survival and

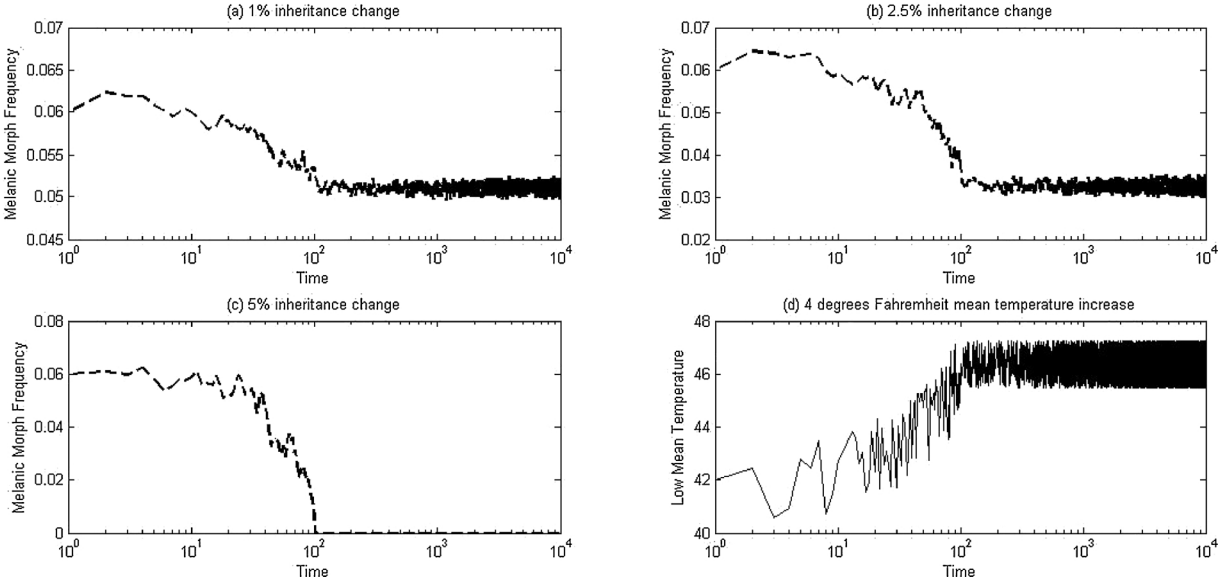

Fig. 3. Melanic morph frequency over time for three different relations between inheritance parameter and temperature for the minimal climate-warming scenario (4° F increase in average temperature is assumed) (a) 1% decrease in the inheritance parameter per a degree Fahrenheit increase in temperature is assumed; (b) 2.5% decrease is assumed; (c) 5% decreased is assumed; (d) mean temperature change starting from 42° F and gradually increasing to 46° F.

reproduction rates compared to the silver morph. The consequence of loss of melanism is the loss of fitness for the black male phenotype/genotype.

While the primary focus of this study was mosquitofish, many fish, insects, mice, and other vertebrates have temperature-sensitive enzymes (Basau et al., 2002; King et al., 1991). An enormous array of insects and vertebrates have dark coloration as a result of melanin expression, and temperature often plays a key role in this expression (True et al., 1999). In Siamese and Burmese cats, temperature-sensitive alleles result in a face-mask and dark pigmentation on extremities (Lyons et al., 2005). Temperature-sensitive alleles also affect melanic expression in fruit flies (O'Grady and DeSalle, 2000) and mice (Kwon et al., 1989). Different colored grasshoppers choose different habitats relating to heating of the body (Ahnesjo and Forsman, 2006).

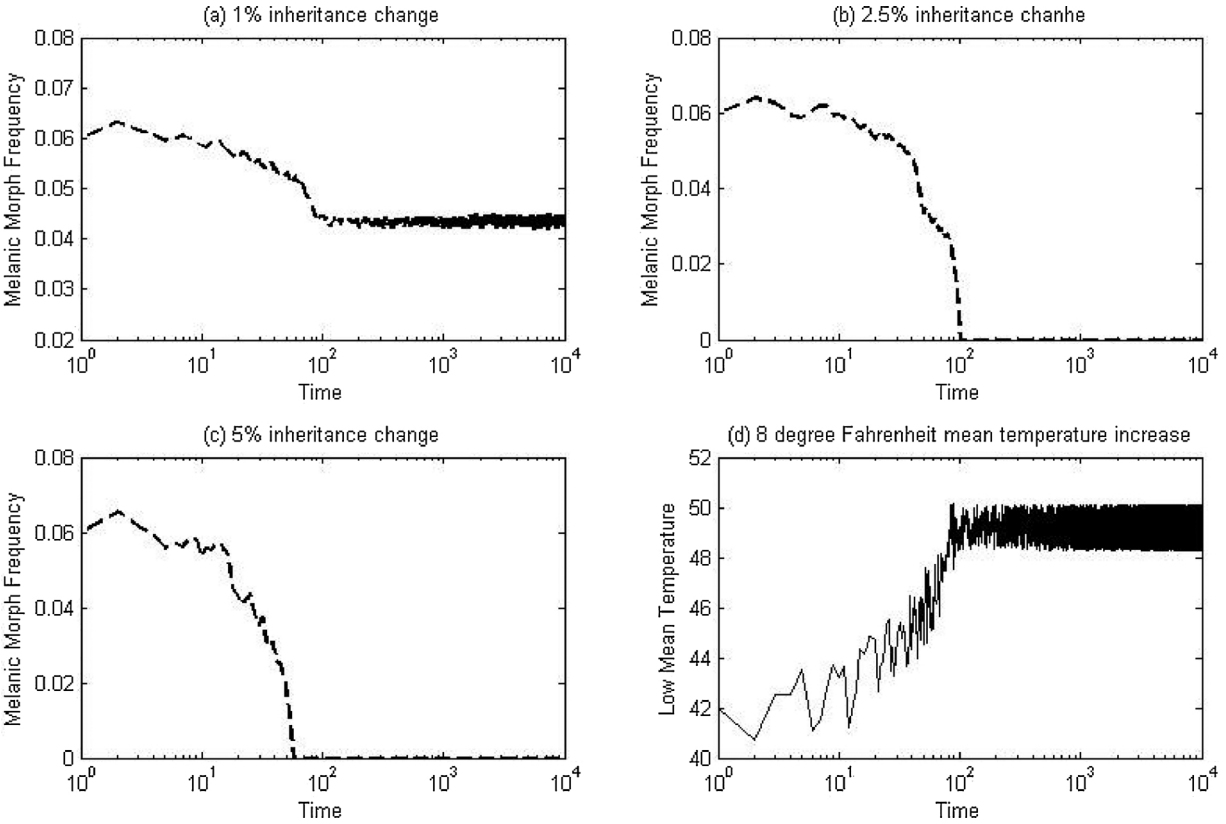

Fig. 4. Melanic morph frequency over time for three different relations between inheritance parameter and temperature for the mid-range climate-warming scenario. (a) 1% decrease in inheritance parameter per a degree Fahrenheit increase in temperature is assumed; (b) 2.5% decrease is assumed; (c) 5% decreased is assumed; (d) temperature change starting from 42° F and gradually increasing to 50° F.

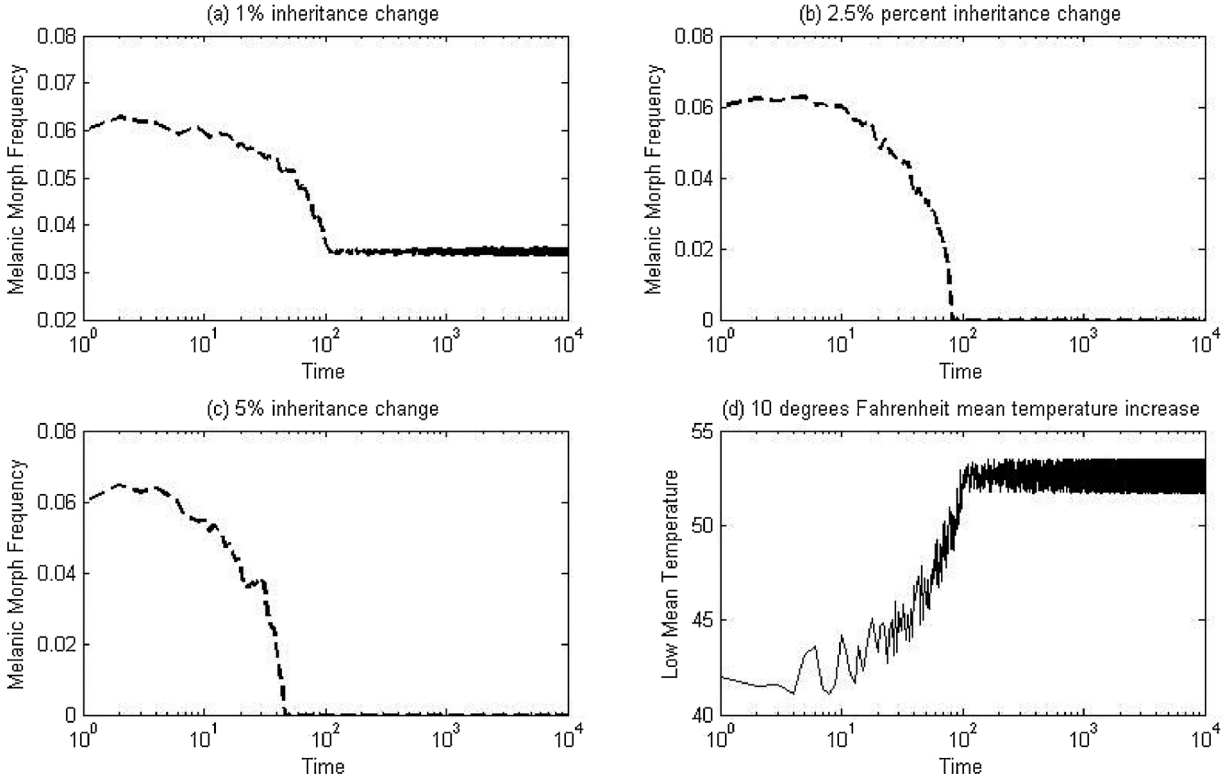

Fig. 5. Melanic morph frequency over time for three different relations between inheritance parameter and temperature for the maximum climate-warming scenario. (a) 1% decrease in inheritance parameter per a degree Fahrenheit increase in temperature is assumed; (b) 2.5% decrease is assumed; (c) 5% decreased is assumed; (d) temperature change starting from 42° F and gradually increasing to 52° F over the first 100 years.

Temperature also affects melanic expression in zebrafish (Kulkeaw et al., 2011) and crickets (Fedorka et al., 2013).

Our study provides an insight about the possible long term effects of increasing temperatures on the melanic mosquitofish population, but this study can also be applied to other organisms that display similar phenotypes that depend upon temperature sensitive enzymes. Our simulations suggest that continued climate change resulting in further mean temperature increase will be devastating to populations dependent on temperature sensitive enzymes for phenotypic expression patterns, which in turn will seriously impact ecological systems and global biodiversity. Studies aiming at furthering our knowledge about predicting the responses of freshwater species to climate variables are particularly important as such information is needed to accommodate freshwater biodiversity in the changing climate and associated environmental changes.

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